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Three new species of *Lachemilla* (Rosaceae) from South America

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Abstract

Three new species of *Lachemilla* (Rosaceae), two from Colombia and one from Peru, are described and illustrated. *Lachemilla rothmaleriana* is characterized by its stout stems, sericeous-villous indumentum, and wide ascending sheaths with trilobate lateral lobes. *Lachemilla argentea* presents a unique combination of tripartite basal leaves with an adaxial silvery villous indumentum, and decumbent branches with verticillate lobed sheaths. Finally, *Lachemilla cyanea* has distinctly basal reniform leaves with a blue-green color and hirsute pubescence. Phylogenetic analyses of the nuclear ribosomal cistron and multiple regions of the plastid genome revealed the allopolyploid origin of the three new taxa.

Resumen

Tres nuevas especies de *Lachemilla* (Rosaceae), dos de Colombia y una de Perú, se describen e ilustran. *Lachemilla rothmaleriana* se caracteriza por tener tallos robustos, indumento sericeo-villoso, y verticilos anchos ascendentes con lóbulos laterales trilobados. *Lachemilla argentea* presenta una combinación única de hojas basales tripartitas con indumento villoso plateado en el haz y ramas decumbentes con verticilos lobulados. Finalmente, *Lachemilla cyanea* presenta hojas basales distintivas de forma reniforme, color azul–verdoso y pubescencia hirsuta. Análisis filogenéticos del cistrón ribosomal nuclear y múltiples regiones del genoma cloroplástico revelaron el origen alopoliploide de los tres nuevos taxones.

Keywords

Allopolyploidy, Colombia, *Lachemilla*, new species, páramo, Peru, Rosaceae

* These authors contributed equally to this work

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Introduction

The genus *Lachemilla* (Focke) Rydb. is a morphologically diverse group that includes perennial herbs, subshrubs, and dwarf shrubs (Romoleroux 1996, 2004; Gaviria 1997). *Lachemilla* is distributed in the neotropical mountains from Mexico to Argentina and Chile, between 2,200 m and 5,000 m (Romoleroux 1996, 2004; Gaviria 1997), and it is especially common and diverse in the high elevation ecosystems of the Northern Andes where this group has undergone a rapid ecological radiation associated with the most recent Andean orogeny (Romoleroux 2004; Morales-Briones et al. 2018a).

The taxonomy of *Lachemilla* has proven challenging (e.g., Perry 1929; Rothmaler 1935a, 1935b, 1937), and although more recent regional treatments have reviewed this group (Gaviria 1997; Romoleroux 2004; Barrie 2015), the complex morphology of *Lachemilla* has obscured species boundaries and morphological subdivisions. Additionally, recent attention to the systematics of *Lachemilla* has resulted in the description of several new species (Romoleroux 2009; Romoleroux and Morales-Briones 2012; Morales-Briones 2016), but a comprehensive monographic revision of the genus is still needed (Romoleroux and Morales-Briones in prep.).

Based on molecular phylogenetic evidence, Morales-Briones et al. (2018a) proposed the recognition of 61 species of *Lachemilla* separated into four well-supported lineages that are somewhat congruent with previously morphology-based classification systems (Perry 1929; Rothmaler 1937). The Tripartite clade includes herbs with ascending and procumbent stems and tripartite leaves. The Verticillate clade includes subshrubs with erect or decumbent stems and reduced leaves that fuse with the stipules to form verticillate sheaths. The Pinnate clade comprises species with repent or decumbent stems and pinnate or bipinnatifid basal leaves. Finally, the Orbiculate clade encompasses species with a stoloniferous habit and palmately lobed leaves, and, it has been established that the Orbiculate clade is of ancient hybrid origin (Morales-Briones et al. 2018b). Moreover, Morales-Briones and Tank (2019a), using copies (or ribotypes) of the nuclear ribosomal (nrDNA) cistron and multiple regions of the plastid genome (cpDNA), showed that at least 30 species of *Lachemilla* are allopolyploids, and that this condition is widespread among the four main clades of this group.

Here, we describe and illustrate three new species of *Lachemilla*, two from Colombia and one from Peru, and using a phylogenetic approach, we show evidence that these new species are of allopolyploid origin.

Materials and methods

Phylogenetic analyses

We used previously published datasets from Morales-Briones and Tank (2019b) from the nrDNA cistron and 45 regions of cpDNA for *Lachemilla*, and included 68 samples representing 48 species of *Lachemilla*, seven samples of the three new taxa, and four outgroups (Appendix 1). DNA extraction, amplification and sequencing were

carried out as described in Morales-Briones and Tank (2019a). Molecular datasets from Morales-Briones and Tank (2019a) and data for the new taxa presented here were generated simultaneously. Data processing and ribotype selection was performed as described in Morales-Briones and Tank (2019a). The three regions of the nrDNA (ETS, ITS1, and ITS2) were concatenated, and the 45 regions of the cpDNA were concatenated as well. Phylogenetic analyses of the nrDNA and cpDNA matrices were carried out independently to avoid conflicting phylogenetic signal due to widespread cytonuclear discordance in *Lachemilla* produced by polyploidy and ancient hybridization (Morales-Briones et al. 2018a, 2018b). Maximum likelihood (ML) analyses were conducted with RAxML v8.2.10 (Stamatakis 2014) using a GTRGAMMA model, 100 searches for the best tree, and clade support was assessed with 1,000 bootstrap replicates summarized using transfer bootstrap expectation (TBE; Lemoine et al. 2018). Bayesian inferences (BI) were performed with MrBayes v3.2.6 (Ronquist et al. 2012) on the CIPRES portal (Miller et al. 2010). Analyses consisted of two independent runs with four Markov Chain Monte Carlo (MCMC) chains for 20 million generations with trees sampled every 20,000th generation and allowing sampling across the entire substitution rate model space using reversible-jump Markov Chain Monte Carlo (rjMCMC) (nst = mixed) and rate variation set to GAMMA. Parameter estimate convergence of the independent MCMC runs was assessed by analyzing plots of all parameters and the –lnL after reaching an ESS (effective-sample size) ≥ 200 using Tracer v1.6 (Rambaut et al. 2014). A 50% majority rule consensus tree was generated and posterior probabilities (PP) were calculated after removing the first 25% of sampled trees. Alignments and phylogenetic trees are available at TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S24437).

Taxonomic analyses

Morphological characters were studied using dried herbarium specimens of *Lachemilla* deposited in ANDES, CAS, COL, F, HUT, HAO, ID, JE, MEXU, MO, NY, QCA, TEX, and USM. Additionally, we reviewed species descriptions and types to determine the existence of the new taxa. The conservation status of the new species was evaluated using the guidelines of the International Union for Conservation of Nature (IUCN 2017).

Results and discussion

Phylogenetic analyses

The final cpDNA concatenated matrix included 65 sequences representing 47 species of *Lachemilla* and four outgroup species, and had an aligned length of 22,000 bp. The ML and BI analyses recovered the same overall topology (Fig. 1). The four major clades within *Lachemilla* are the same as in previous phylogenetic analyses of the genus (Morales-Briones et al. 2018a; Morales-Briones and Tank 2019a). The samples of

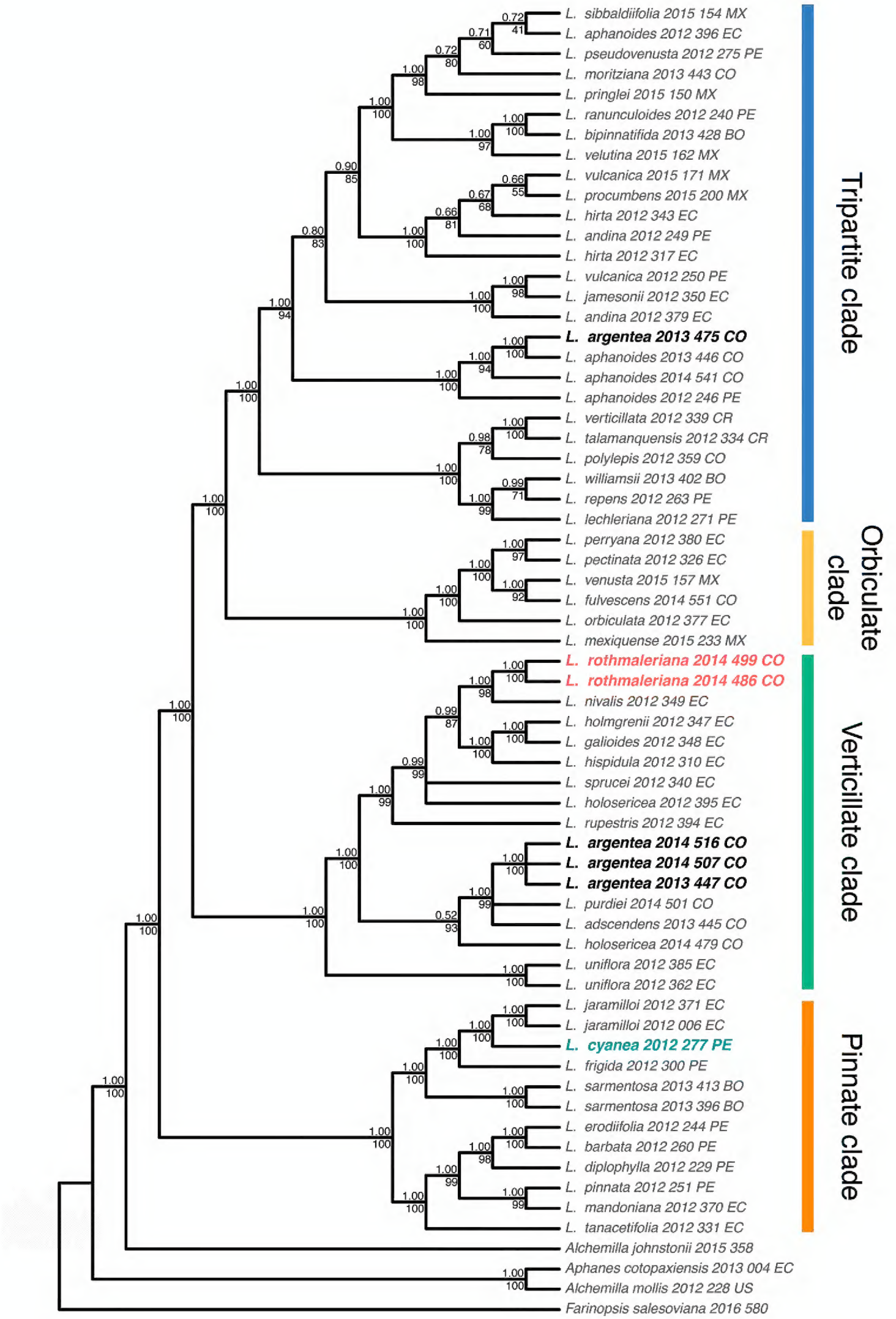
L. sibbaldiifolia 2015 154 MX
L. aphanoides 2012 396 EC
L. pseudovenusta 2012 275 PE
L. moritziana 2013 443 CO
L. pringlei 2015 150 MX
L. ranunculoides 2012 240 PE
L. bipinnatifida 2013 428 BO
L. velutina 2015 162 MX
L. vulcanica 2015 171 MX
L. procumbens 2015 200 MX
L. hirta 2012 343 EC
L. andina 2012 249 PE
L. hirta 2012 317 EC
L. vulcanica 2012 250 PE
L. jamesonii 2012 350 EC
L. andina 2012 379 EC
L. argentea 2013 475 CO
L. aphanoides 2013 446 CO
L. aphanoides 2014 541 CO
L. aphanoides 2012 246 PE
L. verticillata 2012 339 CR
L. talamanquensis 2012 334 CR
L. polylepis 2012 359 CO
L. williamsii 2013 402 BO
L. repens 2012 263 PE
L. lechleriana 2012 271 PE
L. perryana 2012 380 EC
L. pectinata 2012 326 EC
L. venusta 2015 157 MX
L. fulvescens 2014 551 CO
L. orbiculata 2012 377 EC
L. mexiquense 2015 233 MX
L. rothmaleriana 2014 499 CO
L. rothmaleriana 2014 486 CO
L. nivalis 2012 349 EC
L. holmgrenii 2012 347 EC
L. galioides 2012 348 EC
L. hispidula 2012 310 EC
L. sprucei 2012 340 EC
L. holosericea 2012 395 EC
L. rupestris 2012 394 EC
L. argentea 2014 516 CO
L. argentea 2014 507 CO
L. argentea 2013 447 CO
L. purdiei 2014 501 CO
L. adscendens 2013 445 CO
L. holosericea 2014 479 CO
L. uniflora 2012 385 EC
L. uniflora 2012 362 EC
L. jaramilloi 2012 371 EC
L. jaramilloi 2012 006 EC
L. cyanea 2012 277 PE
L. frigida 2012 300 PE
L. sarmentosa 2013 413 BO
L. sarmentosa 2013 396 BO
L. erodiifolia 2012 244 PE
L. barbata 2012 260 PE
L. diplophylla 2012 229 PE
L. pinnata 2012 251 PE
L. mandoniana 2012 370 EC
L. tanacetifolia 2012 331 EC
Alchemilla johnstonii 2015 358
Aphanes cotopaxiensis 2013 004 EC
Alchemilla mollis 2012 228 US
Farinopsis salesoviana 2016 580
Tripartite clade
Orbiculate clade
Verticillate clade
Pinnate clade

Figure 1. Bayesian 50% majority rule consensus tree of the cpDNA dataset. Posterior probabilities and transfer bootstrap expectation support values are shown above and below the branches, respectively.

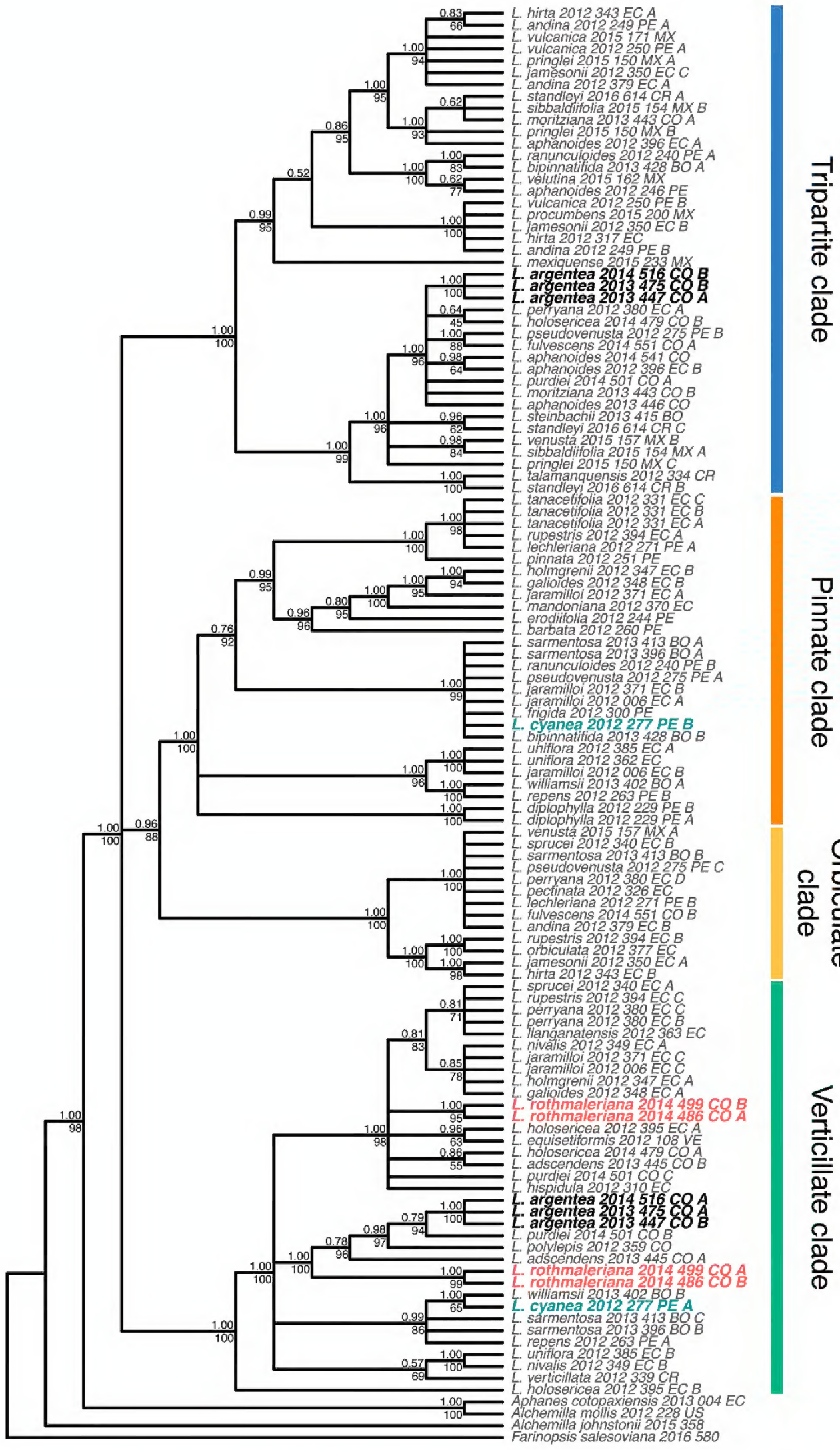
L. hirta 2012 343 EC A
L. andina 2012 249 PE A
L. vulcanica 2015 171 MX
L. vulcanica 2012 250 PE A
L. pringlei 2015 150 MX A
L. jamesonii 2012 350 EC C
L. andina 2012 379 EC A
L. standleyi 2016 614 CR A
L. sibbaldiifolia 2015 154 MX B
L. moritziana 2013 443 CO A
L. pringlei 2015 150 MX B
L. aphanoides 2012 396 EC A
L. ranunculoides 2012 240 PE A
L. bipinnatifida 2013 428 BO A
L. velutina 2015 162 MX
L. aphanoides 2012 246 PE
L. vulcanica 2012 250 PE B
L. procumbens 2015 200 MX
L. jamesonii 2012 350 EC B
L. hirta 2012 317 EC
L. andina 2012 249 PE B
L. mexiquense 2015 233 MX
L. argentea 2014 516 CO B
L. argentea 2013 475 CO B
L. argentea 2013 447 CO A
L. perryana 2012 380 EC A
L. holosericea 2014 479 CO B
L. pseudovenusta 2012 275 PE B
L. fulvescens 2014 551 CO A
L. aphanoides 2014 541 CO
L. aphanoides 2012 396 EC B
L. purdiei 2014 501 CO A
L. moritziana 2013 443 CO B
L. aphanoides 2013 446 CO
L. steinbachii 2013 415 BO
L. standleyi 2016 614 CR C
L. venusta 2015 157 MX B
L. sibbaldiifolia 2015 154 MX A
L. pringlei 2015 150 MX C
L. talamanquensis 2012 334 CR
L. standleyi 2016 614 CR B
L. tanacetifolia 2012 331 EC C
L. tanacetifolia 2012 331 EC B
L. tanacetifolia 2012 331 EC A
L. rupestris 2012 394 EC A
L. lechleriana 2012 271 PE A
L. pinnata 2012 251 PE
L. holmgrenii 2012 347 EC B
L. galioides 2012 348 EC B
L. jaramilloi 2012 371 EC A
L. mandoniana 2012 370 EC
L. erodiifolia 2012 244 PE
L. barbata 2012 260 PE
L. sarmentosa 2013 413 BO A
L. sarmentosa 2013 396 BO A
L. ranunculoides 2012 240 PE B
L. pseudovenusta 2012 275 PE A
L. jaramilloi 2012 371 EC B
L. jaramilloi 2012 006 EC A
L. frigida 2012 300 PE
L. cyanea 2012 277 PE B
L. bipinnatifida 2013 428 BO B
L. uniflora 2012 385 EC A
L. uniflora 2012 362 EC
L. jaramilloi 2012 006 EC B
L. williamsii 2013 402 BO A
L. repens 2012 263 PE B
L. diplophylla 2012 229 PE B
L. diplophylla 2012 229 PE A
L. venusta 2015 157 MX A
L. sprucei 2012 340 EC B
L. sarmentosa 2013 413 BO B
L. pseudovenusta 2012 275 PE C
L. perryana 2012 380 EC D
L. pectinata 2012 326 EC
L. lechleriana 2012 271 PE B
L. fulvescens 2014 551 CO B
L. andina 2012 379 EC B
L. rupestris 2012 394 EC B
L. orbiculata 2012 377 EC
L. jamesonii 2012 350 EC A
L. hirta 2012 343 EC B
L. sprucei 2012 340 EC A
L. rupestris 2012 394 EC C
L. perryana 2012 380 EC C
L. perryana 2012 380 EC B
L. llanganatensis 2012 363 EC
L. nivalis 2012 349 EC A
L. jaramilloi 2012 371 EC C
L. jaramilloi 2012 006 EC C
L. holmgrenii 2012 347 EC A
L. galioides 2012 348 EC A
L. rothmaleriana 2014 499 CO B
L. rothmaleriana 2014 486 CO A
L. holosericea 2012 395 EC A
L. equisetiformis 2012 108 VE
L. holosericea 2014 479 CO A
L. adscendens 2013 445 CO B
L. purdiei 2014 501 CO C
L. hispidula 2012 310 EC
L. argentea 2014 516 CO A
L. argentea 2013 475 CO A
L. argentea 2013 447 CO B
L. purdiei 2014 501 CO B
L. polylepis 2012 359 CO
L. adscendens 2013 445 CO A
L. rothmaleriana 2014 499 CO A
L. rothmaleriana 2014 486 CO B
L. williamsii 2013 402 BO B
L. cyanea 2012 277 PE A
L. sarmentosa 2013 413 BO C
L. sarmentosa 2013 396 BO B
L. repens 2012 263 PE A
L. uniflora 2012 385 EC B
L. nivalis 2012 349 EC B
L. verticillata 2012 339 CR
L. holosericea 2012 395 EC B
Aphanes cotopaxiensis 2013 004 EC
Alchemilla mollis 2012 228 US
Alchemilla johnstonii 2015 358
Farinopsis salesoviana 2016 580
Tripartite clade
Pinnate clade
Orbiculate clade
Verticillate clade

Figure 2. Bayesian 50% majority rule consensus tree of the nrDNA dataset. Posterior probabilities and transfer bootstrap expectation support values are shown above and below the branches, respectively.

L. rothmaleriana form a clade (TBE = 100, PP = 1.0) and are placed as sister to *L. nivalis* (Kunth) Rothm. in the Verticillate clade. *Lachemilla cyanea* is placed in the clade (TBE = 100, PP = 1.0) composed of *L. frigida* (Wedd.) Rothm. and *L. jaramilloi* Romol. & D.F. Morales-B. (a known allopolyploid species) within the Pinnate clade. *Lachemilla argentea* is placed in two major clades. Three samples form a clade (TBE = 100, PP = 1.0) that is placed along other allopolyploid species (*L. purdiei* (L.M. Perry) Rothm., *L. adscendens* (Rothm.) Rothm. and *L. holosericea* (L.M. Perry) Rothm.) within the Verticillate clade. The remaining sample (2013_475_CO) is placed within a clade composed of only samples of *L. aphanoides* (Mutis ex L. f.) Rothm. within the Tripartite clade.

The final nrDNA concatenated alignment included 121 sequences representing 51 species of *Lachemilla* and four outgroup species, and had aligned length of 1038 bp. The ML and BI analyses also recovered the same overall topology (Fig. 2). As in the cpDNA analyses, the four major clades within *Lachemilla* are the same as in previous studies (Morales-Briones et al. 2018a; Morales-Briones and Tank 2019a). *Lachemilla rothmaleriana* showed the presence of two ribotypes within the Verticillate clade. One of the ribotypes is placed as sister (TBE = 100, PP = 1.00) to a clade composed of *L. adscendens*, *L. polylepis* (Wedd.) Rothm., *L. purdiei*, and *L. argentea*. The second copy is placed within a clade (TBE = 98, PP = 0.91) that includes several species with verticillate sheaths along the entire stem, like *L. hispidula* (L.M. Perry) Rothm., *L. equisetiformis* (Trevir.) Rothm., and *L. nivalis*, and several allopolyploid species (e.g. *L. adscendens*, *L. holosericea*, *L. sprucei* (L.M. Perry) Rothm.), but the resolution within this clade is rather uncertain. *Lachemilla cyanea* also presents two ribotype copies. One copy, as in the cpDNA tree, is placed in the clade (TBE = 100, PP = 0.99) composed of *L. frigida* and its allopolyploid species (e.g. *L. jaramilloi*, *L. sarmentosa* (L.M. Perry) Rothm.) within the Pinnate clade. The other ribotype is placed within a clade (TBE = 86, PP = 0.99) composed only of allopolyploid species (*L. williamsii* (L.M. Perry) Rothm., *L. repens* (C. Presl) Rothm., and *L. sarmentosa*) within the Verticillate clade. All samples of *L. argentea* also have two ribotypes. The first is placed in the Tripartite clade along several allopolyploid species that involve *L. aphanoides* as one parental species (e.g. *L. pseudovenusta*, *L. fulvescens* (L.M. Perry) Rothm., *L. purdiei*, *L. perryana* (Rothm.) Rothm.). The second copy is placed as sister (TBE = 84, PP = 0.79) to the allopolyploid species *L. purdiei* in the Verticillate clade.

Previous phylogenetic analysis of *Lachemilla* have shown that allopolyploidy is common in this group with at least 30 species confirmed to be of allopolyploid origin (Morales-Briones and Tank 2019a). Here we show that the three new taxa of *Lachemilla* described here are also allopolyploids. *Lachemilla rothmaleriana* appears to be an allopolyploid of two different species within the Verticillate clade. Based on the cpDNA tree we can determine that *L. nivalis* might be the maternal lineage, while the paternal lineage seems to be the same as in the allopolyploids *L. adscendens*, *L. purdiei* and *L. argentea*, all from Colombia. From the nrDNA tree we can see that the paternal species is either extinct or unsampled. Morphologically, *L. rothmaleriana* presents the main characteristic of the Verticillate clade, which is the presence of reduced leaves that fuse with the stipules to form verticillate sheaths, but this new taxon is distinguished mainly by

the presence of wide ascending sheaths with trilobate lateral lobes and a dense sericeous-villous indumentum (see Taxonomic treatment for details). The presence of divided lobes is a characteristic of other species of the Verticillate clade that are now known to be of hybrid origin, like *L. adscendens* and *L. sprucei* (Morales-Briones and Tank 2019a).

Lachemilla argentea is also an allopolyploid species of two major clades. The cpDNA tree shows that three of the four samples have the maternal lineage from the Verticillate clade, while for one sample (2013_475_CO) the maternal lineage is *L. aphanoides* in the Tripartite clade. The nrDNA data shows that the paternal lineage of *L. argentea* is in the Tripartite clade, except for 2013_475_CO which has an extinct or unsampled parental lineage in the Verticillate clade. Although the sample 2013_475_CO is monophyletic with the other samples of this species for both ribotypes in the nrDNA, the different position in the cpDNA tree is clear evidence that the parental contribution in the formation of allopolyploid species in *Lachemilla* can work in both directions, as well as the recurrent origin of allopolyploids, which has also been previously shown for this group (Morales-Briones and Tank 2019a), and is known for other related groups in Rosaceae, like *Fragaria* (Dillenberger et al. 2018). The basal tripartite leaves of *Lachemilla argentea* are characteristic of the Tripartite clade, but its decumbent branches with verticillate lobed sheaths resemble the Verticillate clade (see Taxonomic treatment for details).

Finally, *L. cyanea* also shows evidence of an allopolyploid origin between two major clades. The maternal species appears to be *L. frigida* in the Pinnate clade, which is also the maternal lineage of *L. jaramilloi* (Morales-Briones and Tank 2019a), with which *L. cyanea* also shares a rosette habit (see Taxonomic treatment for details). The paternal lineage appears to be the same as in the allopolyploid and morphologically similar species *L. williamsii*, *L. repens*, and *L. sarmentosa* in the Verticillate clade, where the parental lineage of these species has been shown likely to be extinct (Morales-Briones and Tank 2019a). Interestingly, these three similar species are hybrids of three different major clades (Pinnate, Verticillate, and Tripartite; Morales-Briones et al. 2018a). Given its tripartite leaf and glomerulate inflorescence (see Taxonomic treatment for details), *L. cyanea* also shares characteristics with the Tripartite clade, but we were not able to obtain evidence of this from the nrDNA tree, which can be explained by omission nrDNA copies during bioinformatic processing of the PCR amplicon pools as seen in other species of *Lachemilla* (Morales-Briones and Tank 2019a).

Taxonomic treatment

Lachemilla rothmaleriana **D.F.Morales-B. & Romol., sp. nov.**
urn:lsid:ipni.org:names:77199640-1
Figs 3–5

Diagnosis. *Lachemilla rothmaleriana* differs from *L. hispidula* (L.M. Perry) Rothm. and *L. nivalis* (Kunth) Rothm. by its stout stems, sericeous-villous indumentum, wide ascending sheaths with trilobate lateral lobes, and a turbinate-campanulate hypanthium.

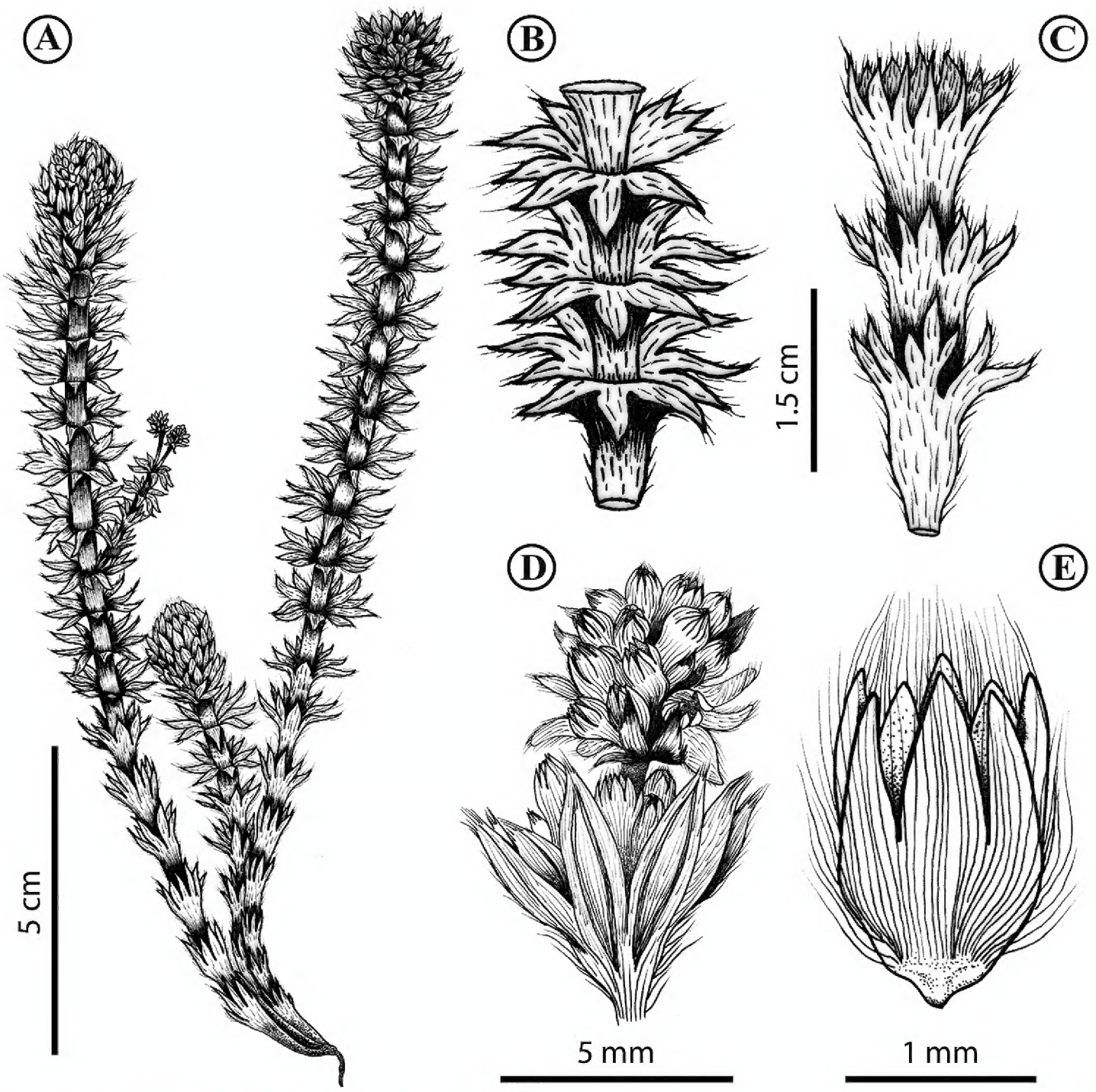

Figure 3. *Lachemilla rothmaleriana*. **A** Habit **B** stem, apical leaves **C** stem, basal leaves **D** flowering branch **E** flower. Illustration by S. Cordero.

Type. COLOMBIA. Boyacá: Duitama. Road to páramo de la Rusia, 22 km from Duitama, before 'fábrica de arepas Buenos Aires', 5.92656N, 73.08826W, alt. 3650 m, 24 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 506.* (holotype: ID!, isotypes: ANDES!, QCA!).

Description. Ascendent subshrubs; stems erect to slightly decumbent, up to 22–27 cm long, robust, densely sericeous-villous, branched at apex. Basal stipules usually caducous, if present 5–6 mm long, adnate to the petiole at base, free at apex, entirely membranous, brown. Basal leaves usually caducous, if present 3–6-lobed, 4–6 × 3–6 mm; basal petiole 3–4 mm long. Distal leaves reduced, adnate, and connate to the distal stipules forming verticillate, lobed sheaths; sheath lobes 7–8, ascending to spreading at maturity, lanceolate, one lobe 3–5 lobate, lobes (4) 6–8 × 1–2 (4) mm, (2/3 of the entire sheath length), chartaceous, margin revolute, lower surface appressed

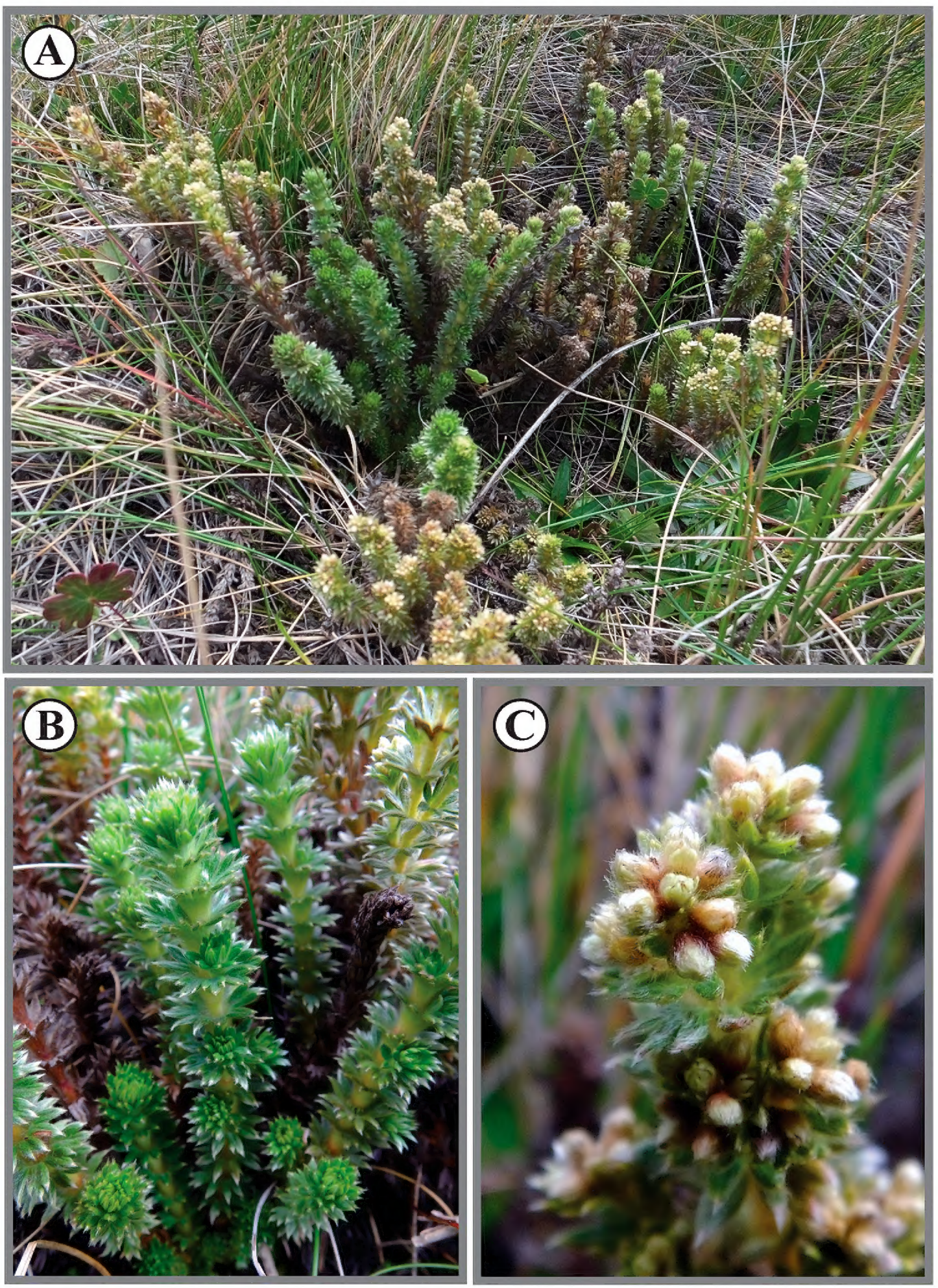

Figure 4. *Lachemilla rothmaleriana*. **A** Habit **B** stems **C** flowering branch.

sericeous-villous to villous, upper surface sericeous-villous to glabrescent. Inflorescences terminal or axilar ± glomerulate cymes; floral bracts lobed, ascending; 8–10 flowers per inflorescence; pedicels 0.3–0.4 mm long, pilose. Flowers 1.5–2.5 mm long; hypan-

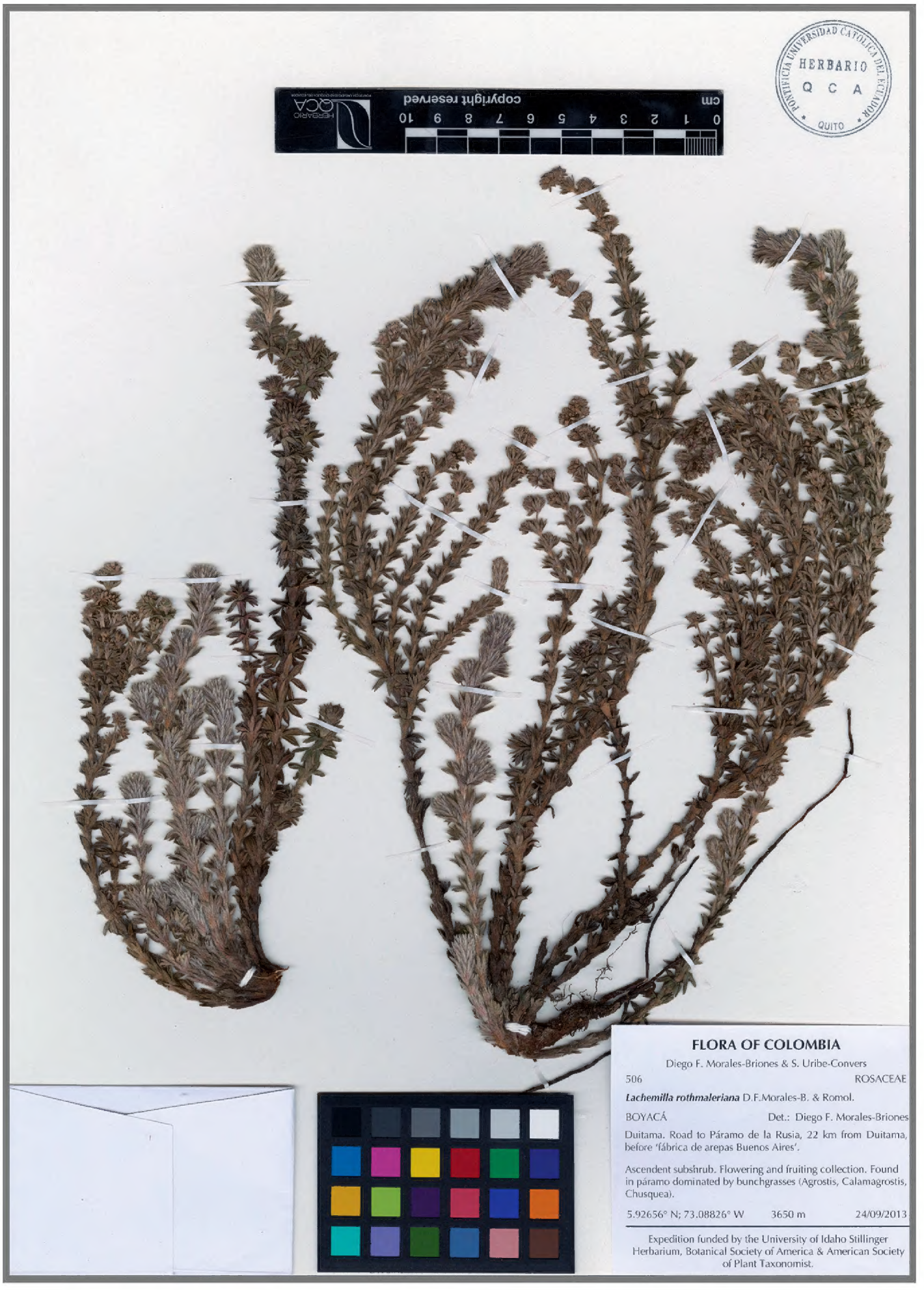
FLORA OF COLOMBIA
Diego F. Morales-Briones & S. Uribe-Convers
506
ROSACEAE
Lachemilla rothmaleriana D.F.Morales-B. & Romol.
BOYACÁ
Det.: Diego F. Morales-Briones
Duitama. Road to Páramo de la Rusia, 22 km from Duitama, before 'fábrica de arepas Buenos Aires'.
Ascendent subshrub. Flowering and fruiting collection. Found in páramo dominated by bunchgrasses (Agrostis, Calamagrostis, Chusquea).
5.92656° N; 73.08826° W
3650 m
24/09/2013
Expedition funded by the University of Idaho Stillinger Herbarium, Botanical Society of America & American Society of Plant Taxonomist.
HERBARIO QCA
PONTIFICIA UNIVERSIDAD CATÓLICA DEL ECUADOR
QUITO
cm
copyright reserved

Figure 5. *Lachemilla rothmaleriana*. Isotype collection: *Morales-Briones D.F. & Uribe-Convers S. 506.* (QCA).

thium turbinate-campanulate, brown-reddish at base, pilose-sericeous outside slightly glabrescent at base, glabrous within; 4 episepals and 4 sepals connivent to ± straight, abaxially sericeous, adaxially glabrous; episepals narrowly ovate, 0.8–1 × 0.2–0.3 mm,

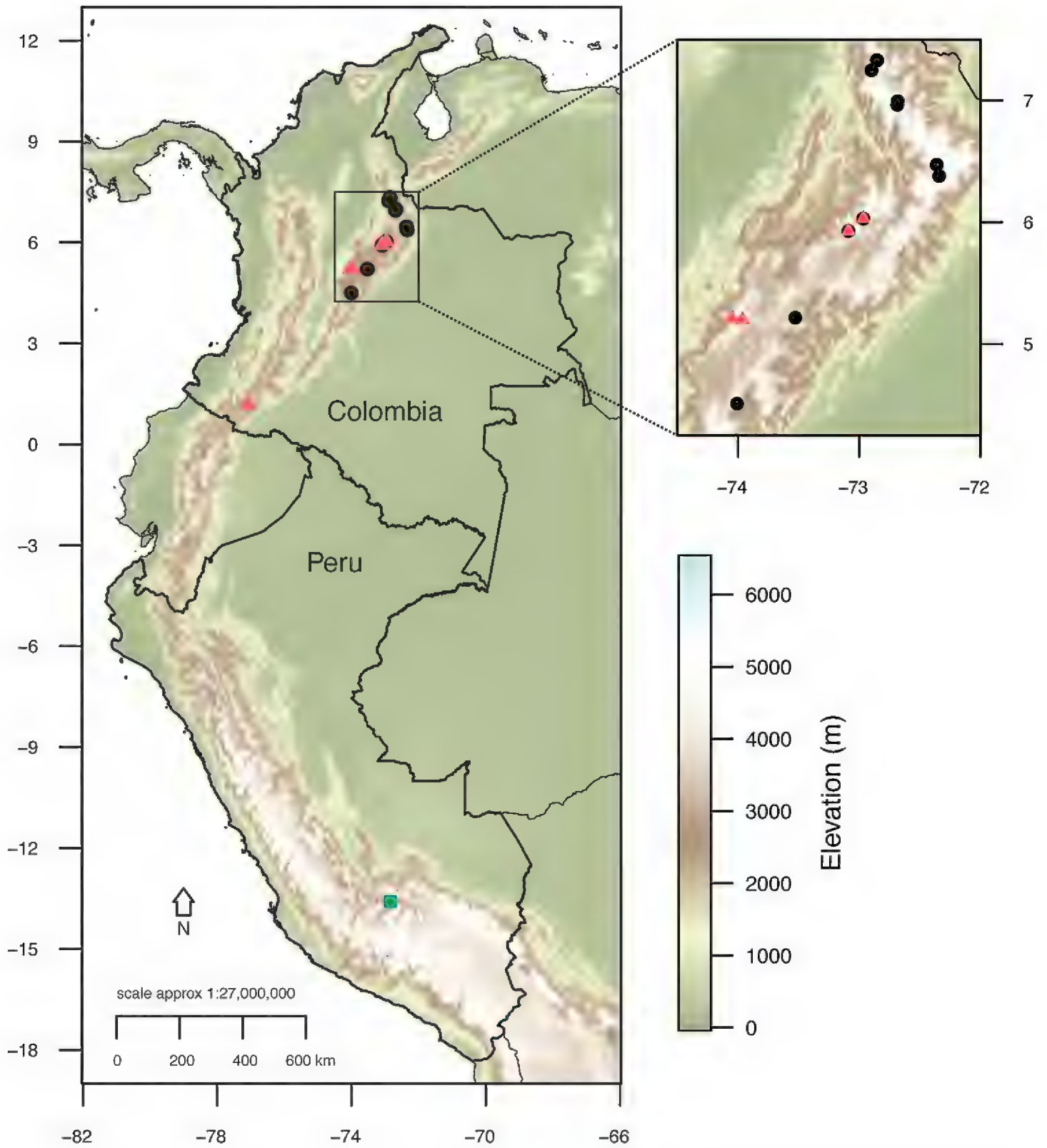

Figure 6. Geographic distribution of *Lachemilla rothmaleriana* (read triangles), *L. argentea* (black circles), and *L. cyanea* (cyan rectangle).

apex acute; sepals ovate, 0.5–1 × 0.4–0.5 mm, apex ± acute; stamens 2 adnate to the floral disc; carpels 2 (3), stigma clavate. Two achenes 0.8–0.9 × ca. 0.5 mm, subovoid.

Distribution and ecology. *Lachemilla rothmaleriana* has a scattered distribution in the northcentral region of the Cordillera Oriental and in the southern part of the Cordillera Central of the Colombian Andes, between 3250 and 3768 m (Fig. 6). This species is mainly found in páramos dominated by bunchgrasses (*Agrostis*, *Calamagrostis*, *Chusquea*) and lives in sympatry with *L. hipidula*, *L. nivalis*, and *L. purdiei*. Flowering and fruiting collections dated from the months of January, May, September, and December.

Etymology. The specific epithet honors Prof. Dr. Werner Rothmaler (1908–1962), a German botanist who studied *Lachemilla* in detail and described over 20 species of this genus.

Conservation status. *Lachemilla rothmaleriana* is known only from the three localities that are zones impacted by human activities, including conversion to agriculture. Following the IUCN (2017) guidelines, based on the reduced geographic distribution and altered land use at the type locality, this species should be categorized as vulnerable (VU).

Additional specimens examined. COLOMBIA. Putumayo: Comisaria del Putumayo, Alta cuenca del río Putumayo, filo de Cordillera entre El Encano y Sibundoy, páramo de San Antonio del Bordoncillo, 1.18333N, 77.1000W, alt. 3250 m, 4 January 1941, *Cuatrecasas J. 11761* (COL, F, JE frag.). **Santander:** Páramo del Consuelo, Belén, Vereda de San José, 18 km from Belén on road to Encino, 6.02920N, 72.96523W, alt. 3768 m, 23 September, 2013, *Morales-Briones D.F. & Uribe-Convers S. 492* (ANDES, ID, QCA).

Notes. *Lachemilla rothmaleriana* resembles *L. hispidula* and *L. nivalis* by its habit and erect stems with reduced leaves that fuse with the stipules to form verticillate sheaths, but differs by having trilobate lateral lobes. Additionally, *L. hispidula* has an overall hispid pubescence, while *L. rothmaleriana* has a characteristic sericeous-villous indumentum. Moreover, *L. rothmaleriana* has a turbinate-campanulate hypanthium with pilose-sericeous pubescence, while *L. hispidula* has a globose-campanulate hypanthium with pilose-hirsute pubescence. *Lachemilla nivalis* has a hypanthium with similar indumentum but its shape is only slightly campanulate. In the shape of sheath lobes, *L. rothmaleriana* somewhat resembles *L. galioides* (Benth.) Rothm., but the latter has slender stems, broader sheath lobes, and villous-hispid indumentum.

Lachemilla argentea D.F.Morales-B. & Romol., sp. nov.

urn:lsid:ipni.org:names:77199641-1

Figs 7–9

Diagnosis. *Lachemilla argentea* differs from *L. holmgrenii* Rothm. and *L. adscendens* (Rothm.) Rothm. by its herbacecous habit with decumbent branches, conspicuous basal reniform tripartite leaves with an adaxial silvery villous pubescence, and a turbinate to urceolate hypanthium with pilose-sericeous pubescence.

Type. COLOMBIA. Bogotá, Distrito Capital: Páramo de Cruz Verde. Path to Laguna El Verjón, 4.56102N, 74.02172W, alt. 3495 m, 26 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 523* (holotype: ID!, isotypes: ANDES!, QCA!).

Description. Decumbent herbs; branches decumbent up to 12 cm long, sericeous-villous. Basal stipules 5–10 mm long, adnate to the petiole, sparsely villous, membranous, brown at base, free at apex. Basal leaves tri-parted, blade reniform in outline, 6–7 (–10) × 7.5–10 (–1.3) mm, 3 lobes, chartaceous, slightly plicate, lobes unequally obovate-rhomboid, margin dentate-incised, teeth 3–6 on each of the lobes, lower sur-

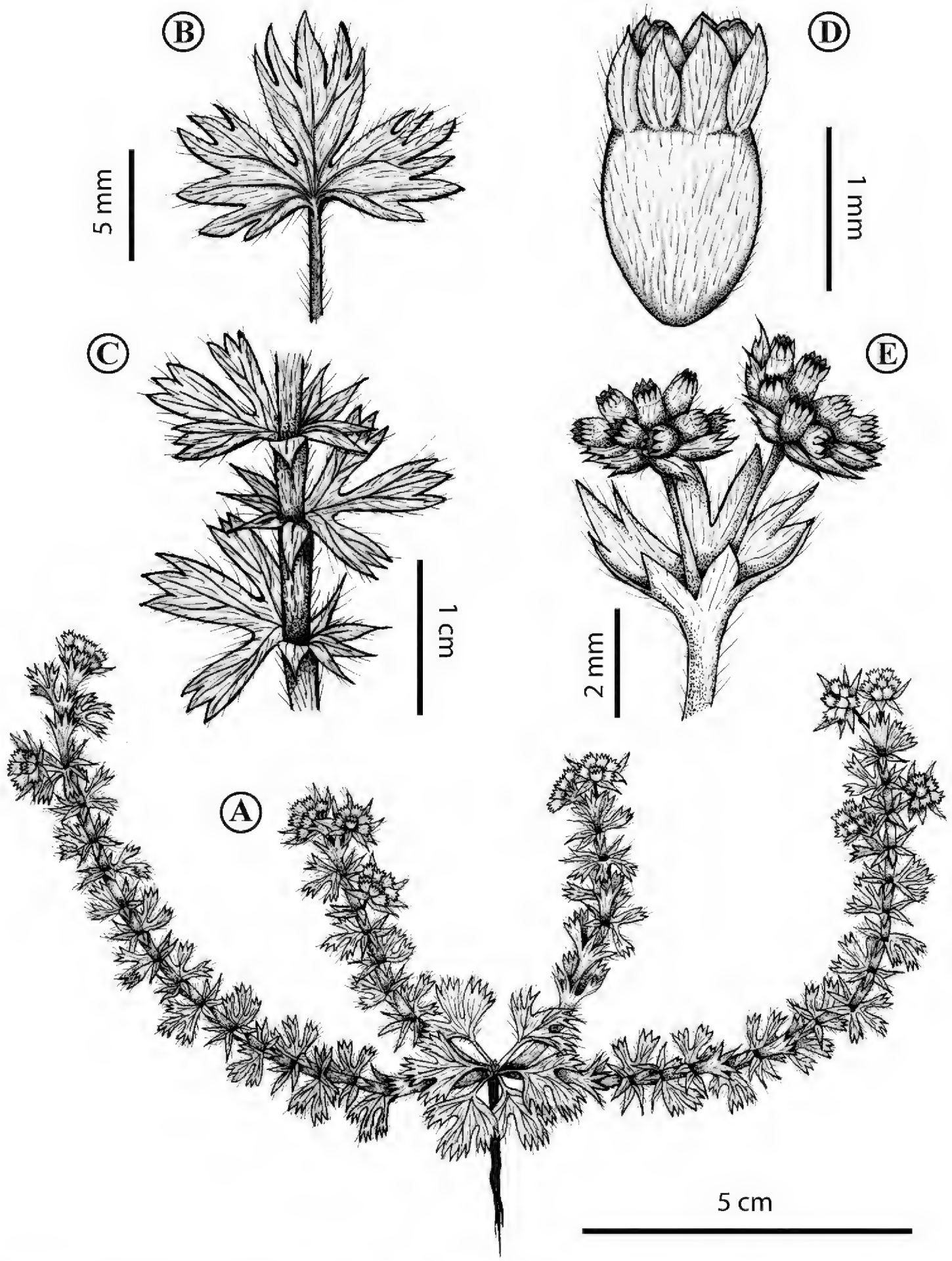

Figure 7. *Lachemilla argentea*. **A** Habit **B** basal leaf **C** stem, apical leaves **D** flower **E** flowering branch. Illustration by C. Rodríguez.

face sparsely sericeous-villous, upper surface villous; basal petiole 5–12 mm long. Distal stipules and distal leaves reduced adnate and connate, forming verticillate lobed sheaths; sheath lobes 6–10 ascending or slightly spreading; lobes 4–7 × 1.5–3 mm,

lanceolate, entire or trilobed, decreasing in size. Inflorescences axilar or terminal glomerulate cymes, flowers aggregate at the distal part. Floral bracts 2–4 mm long, free, incised, and ascending; 3–7 flowers per inflorescence; pedicels 0.5–1 mm long, slightly pilose. Flowers 2–2.5 mm long; hypanthium turbinate to urceolate, green or reddish, pilose-sericeous outside, glabrous within; 4 episepals and 4 sepals green or slightly reddish, straight, abaxially pilose-sericeous, adaxially glabrous; episepals triangular, 0.7–0.8 × 0.4–0. 5 mm, apex acute; sepals triangular-ovate, 0.75–0.85 × 0.5–0.6 mm, apex acute; stamens 2 adnate to the floral disc; carpels 2–3, stigma clavate. Two achenes, ca. 1–1.5 × 0.6–0.8 mm, globose-ovoid.

Additional specimens examined. COLOMBIA. Bogotá, Distrito Capital: Páramo de Cruz Verde, Bogotá-Choachí road, km 11.2, alt. 3257 m, 1 May 1972, *Cleef A. 3330A* (COL). **Bogotá, Distrito Capital:** Páramo de Cruz Verde, path to Laguna El Verjón, 4.56102N, 74.02172W, alt. 3495 m, 26 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 522* (ANDES, ID, QCA). **Boyacá:** Güicán, Sierra Nevada del Cocuy, road to the small house, in 'Lagunilla' area, towards to Púlpito del Diablo, 6.37906N, 72.33995W, alt. 3950 m, 18 September 2013, *Morales-Briones D.F. et al. 476* (ANDES, ID, QCA). **Boyacá:** Duitama, road to Páramo de la Rusia, 22 km from Duitama, before 'fábrica de arepas Buenos Aires', 5.92656N, 73.08826W, alt. 3650 m, 24 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 507* (ANDES, ID, QCA). **Boyacá:** Belén, Vereda de San José, Páramo del Consuelo, 18 km from Belén, on the way to Encino, 6.02920N, 72.96523W, alt. 3768 m, 23 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 499* (ANDES, ID, QCA). **Boyacá:** Páramo de Pisba, Socha-La Punta road, km 72, near to M.O.P campsite. El Cadillal, stony slope, alt. 3500 m, 8 June 1972, *Cleef A. 4235* (COL). **Boyacá:** Páramo NW of Belén, Vereda S. José de la Montaña, Alto de las Cruces and surroundings, alt. 3790 m, 24 February 1972, *Cleef A. 1756* (COL). **Boyacá:** Páramo de Pisva, Socha-La Punta road, km 61, 5.6 km east of Los Pinos, Alto de Granados, alt. 3635 m, 12 June 1972, *Cleef A. 445813* (COL). **Boyacá:** Páramo de Pisva, flank SW of Morros de S. Gabriel, 2 km SW of Laguna Batanera, alt. 3670 m, 18 June 1972, *Cleef A. 4702A* (COL). **Cundinamarca:** Villa Pinzón, Páramo de Guachenque. Entrance to the Laguna del Valle and surroundings of Laguna del Mapa, 5.21641N, 73.52675W, alt. 3346 m, 25 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 514* (ANDES, ID, QCA). **Cundinamarca:** Páramo de Palacio, 18 km from the road, alt. 3485 m, 16 December 1971, *Cleef A. 327* (COL). **Santander:** Vetas, road to the Laguna Pajaritos, at the entrance of private property, 7.33349N, 72.85373W, alt. 3539 m, 14 September 2013, *Morales-Briones D.F. et al. 437* (ANDES, ID, QCA). **Santander:** Vetas, road to Laguna Pajaritos, 7.33086N, 72.85106W, alt. 3585 m, 14 September 2013 *Morales-Briones et al. D.F. 440* (ANDES, ID, QCA). **Santander:** Páramo de Almorzadero, road Presidente-Cerrito, km 98, 6.99470N, 72.68187W, alt. 3567 m, 16 September 2013, *Morales-Briones D.F. et al. 458* (ANDES, ID, QCA). **Santander:** Páramo de Almorzadero, road Presidente-Cerrito, km 98, 6.96333N, 72.68488W, alt. 3801 m, 16 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 459* (ANDES, ID, QCA).

Mixed specimens examined. the following specimens are collections with two different species under the same number, one (a) correspond to *L. argentea*. **Boyacá:**

Figure 8. *Lachemilla argentea*. **A** Habit **B** basal leaves **C** flowering branch.

Páramo de Pisva, Alto de Granados, 5 km E of Los Pinos, alt. 3735m, 15 June 1972, *Cleef A. 4593A* (a) (COL). **Boyacá:** Güicán Sierra Nevada del Cocuy, after Cabañas Kanwara, 17.7 km from 'water plant', Lomas Las Pajas, 6.47093N, 72.35934W,

alt. 4105 m, 17 September 2013, *Morales-Briones D.F. & Uribe-Convers S. 473* (a) (ANDES, ID, QCA). **Santander:** Páramo de Santurbán, Berlín, 7 km from Vetas, 7.24935N, 72.89784W, alt. 3567 m, 13 September 2013, *Morales-Briones D.F. et al. 431* (a) (ANDES, ID, QCA).

Deviating specimens examined. The following specimens have similar habit, leaf shape, and pubescence to *L. argentea*, but they only differ in having glabrous flowers. These specimens may represent only a variety of *L. argentea*, but they are maintained here as uncertain taxa until more material is available or can be included in phylogenetic analyses. **Boyacá:** Páramo NW of Belén, Quebrada Minas. Hoya CLLA, Slopes N of Valle Lajas, alt. 3835m, 2 March 1973, *Cleef A. 2119A* (COL). **Boyacá:** Páramo de Pisva, Road Socha-La Punta, km 61.5, 6 km E from Los Pinos Alto de Granados, alt. 3630 m, 14 June 1972, *Cleef A. 4545* (COL). **Cundinamarca:** Páramo de Palacio aprox. 1 km E from 'la mina de cal', alt. 3853 m, 19 May 1972, *Cleef A. 3853A* (COL). **Quidio/Tolima:** Paramillo of Quindio and Páramo de Tolima. 13 km from Valle de Cocora. 4.64433N, 75.43060W, alt. 3645 m, 4 October 2013, *Morales-Briones D.F. et al. 543* (ANDES, ID, QCA). **Santander:** Vetas, road to Laguna Pajaritos, 7.33086N, 72.85106W, alt. 3585 m, 14 September 2013, *Morales-Briones D.F. et al. 439* (ANDES, ID, QCA).

Distribution and ecology. *Lachemilla argentea* is distributed in the central northern (primarily) regions of the Cordillera Oriental between 3275 and 3735 m (Fig. 6). This species occurs in humid and very humid páramos dominated by grasses, shrubs, and dwarf shrubs. *Lachemilla argentea* can be found living in sympatry with multiple species of *Lachemilla*, including *L. aphanoides*, *L. hispidula*, *L. nivalis*, *L. mandoniana* (Wedd.) Rothm., *L. purdiei*, and *L. vulcanica* (Schltdl. & Cham.) Rydb. Flowering and fruiting collections dated from the months of February, May, June, and September.

Etymology. The specific epithet refers to the silvery aspect of the basal leaves.

Conservation status. *Lachemilla argentea* is a common element throughout its distributional range, and occurs in several well-conserved areas. Following the IUCN (2017) guidelines, we consider this species is not at risk and should be categorized as least concern (LC). Nonetheless, the rapid deterioration and conversion to agriculture of proximate areas where *L. argentea* occurs may put this species at some threat in the near future.

Notes. *Lachemilla argentea* resembles *L. holmgrenii* and *L. adscendens* by having basal tripartite leaves and stem leaves fused to the stipules forming verticillate sheaths with one tripartite lobe that is larger than the remaining lobes, but differs in having an herbaceous habit with decumbent branches, while the other two species are subshrubs with suberect to ascending branches. Furthermore, *L. argentea* has conspicuous basal reniform tripartite leaves with an adaxial silvery villous pubescence, while *L. holmgrenii* and *L. adscendens* have smaller hirsute leaves. These species also vary in the number of sheath lobes; *L. argentea* has 6–10 ascending or slightly spreading lobes, while *L. holmgrenii* and *L. adscendens* have 5–7 loosely ascending to reflexed lobes, and eight erecto-patent lobes, respectively. By having conspicuous basal leaves, *L. argentea* also resembles *L. sprucei*, but the latter is a subshrub with suberect stems and coriaceous 5-parted basal leaves, in addition to distinct 3-parted distal leaves.

HERBARIO
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FLORA OF COLOMBIA
Diego F. Morales-Briones & S. Uribe-Convers
523
ROSACEAE
Lachemilla argentea D.F.Morales-B. & Romol.
BOGOTÁ, D.C.
Det.: Diego F. Morales-Briones
Páramo de Cruz Verde. Path to Laguna El Verjón.
Decumbent herb. Flowering and fruiting collection. Found in very humid páramo dominated by grasses, shrubs, and dwarf shrubs.
4.56102° N; 74.02172° W
3495 m
26/09/2013
Expedition funded by the University of Idaho Stillinger Herbarium, Botanical Society of America & American Society of Plant Taxonomist.
copyright reserved
cm

Figure 9. *Lachemilla argentea*. Isotype collection: *Morales-Briones D.F. & Uribe-Convers S. 523* (QCA).

Key to *Lachemilla rothmaleriana*, *L. argentea*, and similar species of the Verticillate clade from Colombia

Notes. Includes species with stem leaves fused to the stipules forming verticillate sheaths (sect. *Nivales* and sect. *Subnivales*; *sensu* Rothmaler 1935a). Accepted taxa and synonymy follows Morales-Briones et al. (2018a). Adapted in part from Perry (1929) and Romoleroux (2004).

1 Subshrubs with erect or decumbent stems; basal leaves caducous or sessile when present; stem leaves reduced, with the adnate stipule forming verticillate sheaths along the entire stem **2**

– Herbs with procumbent or decumbent stems, or subshrubs with suberect or ± decumbent stems; basal leaves petiolate; lower stem leaves subequal to or often longer than the stipules, 3-parted or 3-lobed, uppermost stem leaves reduced, with the adnate stipule forming verticillate sheaths **8**

2 Outer surface of sheath lobes glabrous or puberulent; lobes 4–6 ..... **3**

– Outer surface of sheath lobes conspicuously pubescent; lobes 4–15 ..... **4**

3 Outer surface of sheath lobes glabrous and reticulate, margins strongly revolute . ..... ***L. equisetiformis***

– Outer surface of sheath lobes hispidulous and not reticulate, margins revolute at apex ..... ***L. ericoides***

4 Plants pilose, villous or sericeous; sheath lobes laxly ascending to erect, basal leaves mainly caducous **5**

– Plants hispid, hirsute or villous; sheath lobes widely spreading to abruptly reflexed; basal leaves usually present (except in *L. verticillata*) **6**

5 Stems sparsely villous, pilose to glabrescent, or sericeous; sheath lobes 10–15, linear to linear-lanceolate, all lobes entire ..... ***L. nivalis***

– Stems densely sericeous-villous; sheath lobes 7–8, lanceolate, one lobe 3–5 lobate ..... ***L. rothmaleriana***

6 Sheath lobes 7–8 (10); stems villous; sepals and episepals divergent and equal in length; hypanthium villous ..... ***L. verticillata***

– Sheath lobes 9–13; stems hispid or hirsute; sepals and episepals connivent, episepals usually a little shorter than the sepals 7

7 Plant copiously hirsute; sheath lobes reflexed; hypanthium glabrous ... ***L. galioides***

– Plant sparsely hispid; sheath lobes spreading; hypanthium glabrous or pubescent ..... ***L. hispidula***

8 Caespitose herbs; stems procumbent or slightly decumbent, multiple branched and rooting **9**

– Herbs or subshrubs; stems suberect or ± decumbent, not branched and not rooting **10**

9 Flowers ca. 2–2.5 mm long, hypanthium campanulate, appressed villous, carpels 5–10; stigma clavate ..... ***L. holosericea***

– Flowers ca. 3.5 mm long, hypanthium globose-urceolate, sericeous-villous, carpels 5; stigma subclavate ..... ***L. purdiei***

10 Basal leaves 5-parted, coriaceous; flowers ca. 2.5–3.5 long; carpels 5–6 ... ***L. sprucei***
– Basal leaves 3-parted, not coriaceous; flowers ca. 2–2.5 long; carpels 2–4 ..... **11**
11 Herbs, sericeous-villous; stems decumbent; sheath lobes 6–10, ascending or slightly spreading ..... ***L. argentea***
– Subshrubs, villous or hirsute; stems suberect or ascending, sheath lobes 5–8, loosely ascending to reflex **12**
12 Stems suberect; sheath lobes 5–7; hypanthium campanulate-globose; carpels 2–3 ..... ***L. holmgrenii***
– Stems ascending; sheath lobes 8; hypanthium globose-urceolate; carpels 3–4 ..... ***L. adscendens***

***Lachemilla cyanea* D.F.Morales-B. & Romol., sp. nov.**
urn:lsid:ipni.org:names:77199642-1
Figs 10–12

Diagnosis. *Lachemilla cyanea* differs from *L. ranunculoides* (L.M. Perry) Rothm. and *L. williamsii* (L.M. Perry) Rothm by its hirsute pubescence, reniform basal leaves that have a blue-green color, and turbinate-campanulate hypanthium.

Type. PERU. Apurímac: Abancay Province, road Abancay - Cuzco, 23 km from Abancay, 13.59722S, 72.84083W, alt. 3423 m, 25 June 2012, *Morales-Briones D.F. & Uribe-Convers S. 246*, (holotype: ID!, isotypes: HAO!, QCA!).

Description. Rosette herbs up to 10 cm long, branches decumbent, sparsely hirsute. Basal stipules 10 mm long, adnate to the petiole, sparsely hirsute, membranaceous, brown at base, free at apex. Basal leaves tri-parted, blade reniform in outline, 17–20 × 25–26 mm, 3 lobes, chartaceous, slightly plicate, lobes unequally obovate-rhomboid, lateral lobes divided the length 1/2 of the blade, margin dentate-incised, teeth 8–10 on each of the lobes, lower and upper surface sparsely hirsute-villous; basal petiole 12–20 mm long. Distal stipules 7–8 mm long, connate and adnate to the petiole at base, free and incised at apex, leaf-like in texture. Distal leaves tri-parted, 8–10 × 8–12 mm, lobes obovate-rhomboid, decreasing in size; distal petiole 1–2.5 mm long. Inflorescences axilar or terminal glomerulate cymes, flowers aggregate at the distal part. Floral bracts 1–2 mm long, free, incised, and ascending to slightly spreading; 2–6 flowers per inflorescence; pedicels 0.6–1 mm long, sericeous. Flowers 2–2.5 mm long; hypanthium turbinate-campanulate, green, glabrous outside and within; 4 episepals and sepals green to reddish at apex, straight, abaxially and adaxially glabrous; episepals triangular, 0.7–0.8 × 0.3–0.4 mm, apex acute; sepals triangular-ovate, 0.7–0.8 × 0.5 mm, apex acute; stamens 2 adnate to the floral disc; carpels 2, stigma clavate. Two achenes, ca. 1 × 0.7–0.8 mm, globose-ovoid.

Distribution and ecology. *Lachemilla cyanea* is only known from the Province of Abancay in the Department of Apurímac at ca. 3420 m in southern Peru (Fig. 6). This species occurs in the transition zone between the montane forest and the high-elevation grassland dominated by dwarf shrubs and herbs. This species lives in sympatry with *L. aphanoides* and *L. fulvescens*. It was collected in flower and fruit in late June.

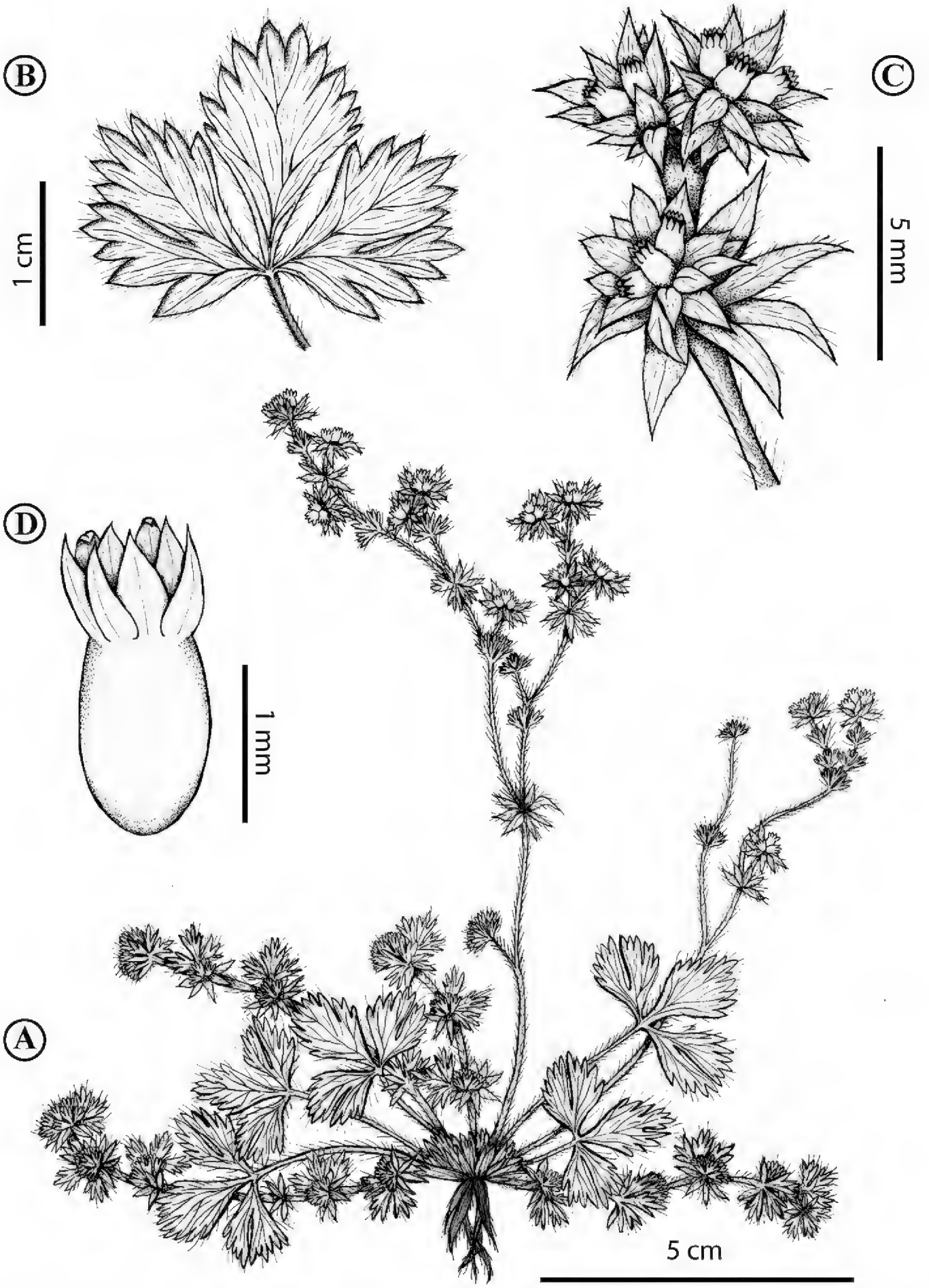

Figure 10. *Lachemilla cyanea.* **A** Habit **B** basal leaf **C** flowering branch **D** flower. Illustration by C. Rodríguez.

Etymology. The specific epithet refers to the blue-green color of the leaves.

Conservation status. *Lachemilla cyanea* is only known from the type locality in a zone severely impacted by human activities, including conversion to agriculture. Fol-

Figure 11. *Lachemilla cyanea*. **A** Habit **B** flowering branch.

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FLORA OF PERU
Diego F. Morales-Briones & S. Uribe-Convers
246
ROSACEAE
Lachemilla cyanea D.F.Morales-B. & Romol.
APURÍMAC
Det.: Diego F. Morales-Briones
Abancay Province, road Abancay-Cuzco, 23 km from Abancay.
Rosette herb. Flowering and fruiting collection. Found in a high-elevation grassland dominated by dwarf shrubs and herbs.
13.59722° S; 72.84083° W
3836 m
25/06/2012
Expedition funded by University of Idaho Stillinger Herbarium.

Figure 12. *Lachemilla cyanea*. Isotype collection: *Morales-Briones D.F. & Uribe-Convers S. 246* (QCA).

lowing the IUCN (2017) guidelines, based on the reduced geographic distribution and altered land use at the type locality, this species should be categorized as endangered (EN), at least until other populations are discovered.

Notes. *Lachemilla cyanea* resembles *L. ranunculoides* in habit and glabrous flower, but differs in the reniform shape of the basal leaves in contrast to the orbicular-ovate shape of the latter. Moreover, *L. cyanea* has a turbinate-campanulate hypanthium while *L. ranunculoides* has an oblong-ventricose hypanthium. *Lachemilla cyanea* also resembles *L. aphanoides* in the tripartite basal leaves and glomerulate inflorescence, but differs in the rosette habit and decumbent branches, in contrast to the erect stems of *L aphanoides*. *Lachemilla cyanea* is also similar to *L. williamsii* in habit, but the former has an overall hirsute pubescence and glabrous flowers with strictly two stamens, while the latter has a general villous pubescence, and villous flowers with up to four stamens (a characteristic only known in *L. williamsii*).

Key to *Lachemilla cyanea* and similar species from the Central Andes

Notes. Includes species with a general prostrate habit, tripartite basal leaves, and mainly glomerulate inflorescences (series *Aphanoides*, subseries 2; *sensu* Perry 1929). Accepted taxa and synonymy follows Morales-Briones et al. (2018a). Adapted from Perry (1929).

1 Herbs with creeping stems, mat-forming; lateral segments of the leaves entire; inflorescences loosely dichotomous; stipules entirely membranaceous.....***L. rupestris***

– Herbs with prostrate or loosely decumbent stems, villous or hirsute; lateral segments of the leaves variously lobed; inflorescences glomerulate cymes; stipules herbaceous at least at apex.....**2**

2 Basal leaves lobes acute; flowers ca. 3 mm long, hirsute-villous to sericeous; stamens 2–4 ..... ***L. williamsii***

– Basal leaves lobes obtuse; flowers ca. 2–2.5 mm long, glabrous or with scattering hairs on the hypanthium lobes; stamens 2.....**3**

3 Plants densely sericeous-villous; sepals oblong-ovate..... ***L. grisebachiana***

– Plants hirsute or glabrate; sepals ovate **4**

4 Basal leaves subreniform; cauline leaves mainly subsessile; episepals reduced or absent; carpels 1–2 .....***L. frigida***

– Basal leaves orbicular or reniform; cauline leaves mainly petiolate; episepals conspicuous, carpels 2–4 .....**5**

5 Basal leaf blade reniform; hypanthium turbinate-campanulate; carpels 2 .... ***L. cyanea***

– Basal leaf blade orbicular; hypanthium oblong-ventricose; carpels 2–4..... .....***L. ranunculoides***

Acknowledgements

We are grateful to the curators of ANDES, CAS, COL, F, MEXU, HUT, HAO, ID, JE, MO, NY, QCA, TEX and USM for access or loans of their collections. We also thank Santiago Cordero and Carla Rodríguez for the illustrations, Daniela Cevallos for the Type images, and Simon Uribe-Convers for assistance during fieldwork. Funding for this work was provided by a Secretaría de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT) doctoral scholarship sponsored by the Instituto Nacional de Biodiversidad (INABIO) to D.F.M-B., Graduate Student Research Grants from the Botanical Society of America (BSA), the American Society of Plant Taxonomists (ASPT), the International Association of Plant Taxonomist (IAPT), and the University of Idaho Stillinger Herbarium Expedition Funds to DFM-B, and a National Science Foundation Doctoral Dissertation Improvement Grant to DCT for DFM-B (DEB-1502049). KR was funded by the Pontificia Universidad Católica del Ecuador and the SENESCYT's 'Arca de Noé' Initiative-Project. Access to genomic and computational resources was granted through the University of Idaho Institute for Bioinformatics and Evolutionary Studies (IBEST) supported by an Institutional Development Award (IDeA) from the National Institute of General Medical Sciences of the National Institutes of Health (P30 GM103324).

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Appendix I

Species and vouchers used in the phylogenetic analyses. Arranged by *species name* and authority, DNA number, and *collector and number* (herbarium code).

Outgroup: ***Alchemilla johnstonii*** Oliv.: 2015_358, *B. Gehrke 364* (UZH). ***Alchemilla mollis*** (Buser) Rothm.: 2012_228_US, *D.F. Morales-Briones 687* (ID). ***Aphanes cotopaxiensis*** Romol. & Frost-Ols.: 2013_004_EC, *D.F. Morales-Briones 276* (ID). ***Farinopsis salesoviana*** (Stephan) Chrtek & Soják: 2016_580, *B. Bartholomew 8364* (MO). **Ingroup:** ***Lachemilla adscendens*** (Rothm.) Rothm.: 2013_445_CO, *D.F. Morales-Briones & S. Uribe-Convers 429A* (ID). ***Lachemilla andina*** (L.M. Perry) Rothm.: 2012_249_PE, *D.F. Morales-Briones & S. Uribe-Convers 218* (ID); 2012_379_EC, *D.F. Morales-Briones et al. 122* (QCA). ***Lachemilla aphanoides*** (Mutis ex L. f.) Rothm.: 2012_246_PE, *D.F. Morales-Briones & S. Uribe-Convers 215* (ID); 2012_396_EC, *D.F. Morales-Briones et al. 115* (QCA); 2013_446_CO, *D.F. Morales-Briones & S. Uribe-Convers 430* (ID); 2014_541_CO, *D.F. Morales-Briones & S. Uribe-Convers 550* (ID). ***Lachemilla argentea*** D.F. Morales-B. & Romol.: 2013_447_CO, *D.F. Morales-Briones et al. 431* (ID); 2013_475_CO, *D.F. Morales-Briones et al. 459* (ID); 2014_507_CO, *D.F. Morales-Briones & S. Uribe-Convers 514* (ID); 2014_516_CO, *D.F. Morales-Briones & S. Uribe-Convers 523* (ID). ***Lachemilla barbata*** (C. Presl) Rothm.: 2012_260_PE, *D.F. Morales-Briones & S. Uribe-Convers 229* (ID). ***Lachemilla bipinnatifida*** (L.M. Perry) Rothm.: 2013_428_BO, *D.F. Morales-Briones et al. 326* (ID). ***Lachemilla cyanea*** D.F. Morales-B. & Romol.: 2012_277_PE, *D.F. Morales-Briones & S. Uribe-Convers 246* (ID). ***Lachemilla diplophylla*** (Diels) Rothm.: 2012_229_PE, *D.F. Morales-Briones & S. Uribe-Convers 198* (ID). ***Lachemilla equisetiformis*** (Trevir.) Rothm.: 2012_108_VE, *A.J.P. Martin 740* (QCA). ***Lachemilla erodiifolia*** (Wedd.) Rothm.: 2012_244_PE, *D.F. Morales-Briones & S. Uribe-Convers 213* (ID). ***Lachemilla frigida*** (Wedd.) Rothm.: 2012_300_PE, *D.F. Morales-Briones & S. Uribe-Convers 269* (ID). ***Lachemilla fulvescens*** (L.M. Perry) Rothm.: 2014_551_CO, *D.F. Morales-Briones & S. Uribe-Convers 560* (ID). ***Lachemilla galioides*** (Benth.) Rothm.: 2012_348_EC, *K. Romoleroux et al. 4403* (QCA). ***Lachemilla hirta*** (L.M. Perry) Rothm.: 2012_317_EC, *K. Romoleroux et al. 4588* (QCA); 2012_343_EC, *K. Romoleroux et al. 4389* (QCA). ***Lachemilla hispidula*** (L.M. Perry) Rothm.: 2012_310_EC, *K. Romoleroux et al. 4470* (QCA). ***Lachemilla holmgrenii*** Rothm.: 2012_347_EC, *K. Romoleroux et al. 4397* (QCA). ***Lachemilla holosericea*** (L.M. Perry) Rothm.: 2012_395_EC, *D.F. Morales-Briones & K. Romoleroux 161* (QCA); 2014_479_CO, *D.F. Morales-Briones et al. 485* (ID). ***Lachemilla jamesonii*** (L.M. Perry) Rothm.: 2012_350_EC, *K. Romoleroux et al. 4387* (QCA). ***Lachemilla jaramilloi*** Romol. & D.F. Morales-B.: 2012_006_EC, *D.F. Morales-Briones & S. Uribe-Convers 193* (ID); 2012_371_EC, *D.F. Morales-Briones et al. 115* (QCA). ***Lachemilla lechleriana*** (Griseb.) Rothm.: 2012_271_PE, *D.F. Morales-Briones & S. Uribe-Convers 240* (ID). ***Lachemilla llanganatensis*** Romol.: 2012_363_EC, *D.F. Morales-Briones et al. 105* (QCA). ***Lachemilla mandoniana*** (Wedd.) Rothm.:

2012_370_EC, *D.F. Morales-Briones et al. 114* (QCA). ***Lachemilla mexiquense*** D.F. Morales-B.: 2015_233_MX, *D.F. Morales-Briones & P. Tenorio-Lezama 683* (ID). ***Lachemilla moritziana*** Dammer: 2013_443_CO, *D.F. Morales-Briones & S. Uribe-Convers 427* (ID). ***Lachemilla nivalis*** (Kunth) Rothm.: 2012_349_EC, *D.F. Morales-Briones & M.F. Latorre-Barragán 11* (QCA). ***Lachemilla orbiculata*** (Ruiz & Pav.) Rydb.: 2012_377_EC, *D.F. Morales-Briones et al. 121* (QCA). ***Lachemilla pectinata*** (Kunth) Rothm.: 2012_326_EC, *K. Romoleroux et al. 4706* (QCA). ***Lachemilla perryana*** (Rothm.) Rothm.: 2012_380_EC, *D.F. Morales-Briones et al. 123* (QCA). ***Lachemilla pinnata*** (Ruiz & Pav.) Rothm.: 2012_251_PE, *D.F. Morales-Briones & S. Uribe-Convers 220* (ID). ***Lachemilla polylepis*** (Wedd.) Rothm.: 2012_359_CO, *P. Sklenář FAA652* (PRC). ***Lachemilla pringlei*** Rydb.: 2015_150_MX, *D.F. Morales-Briones & P. Tenorio-Lezama 595* (ID). ***Lachemilla procumbens*** (Rose) Rydb.: 2015_200_MX, *D.F. Morales-Briones & P. Tenorio-Lezama 648* (ID). ***Lachemilla pseudovenusta*** (Rothm.) Rothm.: 2012_275_PE, *D.F. Morales-Briones & S. Uribe-Convers 244* (ID). ***Lachemilla purdiei*** (L.M. Perry) Rothm.: 2014_501_CO, *D.F. Morales-Briones & S. Uribe-Convers 508* (ID). ***Lachemilla ranunculoides*** (L.M. Perry) Rothm.: 2012_240_PE, *D.F. Morales-Briones & S. Uribe-Convers 209* (ID). ***Lachemilla repens*** (C. Presl) Rothm.: 2012_263_PE, *D.F. Morales-Briones & S. Uribe-Convers 232* (ID). ***Lachemilla rothmaleriana*** D.F. Morales-B. & Romol.: 2014_486_CO, *D.F. Morales-Briones & S. Uribe-Convers 492* (ID); 2014_499_CO, *D.F. Morales-Briones & S. Uribe-Convers 506* (ID). ***Lachemilla rupestris*** (Kunth) Rothm.: 2012_394_EC, *D.F. Morales-Briones et al. 157* (QCA). ***Lachemilla sarmentosa*** (L.M. Perry) Rothm.: 2013_396_BO, *D.F. Morales-Briones et al. 292* (ID); 2013_413_BO, *D.F. Morales-Briones et al. 309* (ID). ***Lachemilla sibbaldiifolia*** (Kunth) Rydb.: 2015_154_MX, *D.F. Morales-Briones & P. Tenorio-Lezama 599* (ID). ***Lachemilla sprucei*** (L.M. Perry) Rothm.: 2012_340_EC, *K. Romoleroux et al. 4474* (QCA). ***Lachemilla standleyi*** (L.M. Perry) Rothm.: 2016_614_CR, *K. Romoleroux et al. 5023* (QCA). ***Lachemilla steinbachii*** Rothm.: 2013_415_BO, *D.F. Morales-Briones et al. 311* (ID). ***Lachemilla talamanquensis*** Romol. & D.F. Morales-B.: 2012_334_CR, *K. Romoleroux et al. 5008* (QCA). ***Lachemilla tanacetifolia*** Rothm.: 2012_331_EC, *K. Romoleroux et al. 4396* (QCA). ***Lachemilla uniflora*** Maguire: 2012_362_EC, *D.F. Morales-Briones et al. 75* (QCA); 2012_385_EC, *D.F. Morales-Briones et al. 130* (QCA). ***Lachemilla velutina*** (S. Watson) Rydb.: 2015_162_MX, *D.F. Morales-Briones & P. Tenorio-Lezama 607* (ID). ***Lachemilla venusta*** (Schltdl. & Cham.) Rydb.: 2015_157_MX, *D.F. Morales-Briones & P. Tenorio-Lezama 602* (ID). ***Lachemilla verticillata*** (Fielding & Gardner) Rothm.: 2012_339_CR, *K. Romoleroux et al. 5007* (QCA). ***Lachemilla vulcanica*** (Schltdl. & Cham.) Rydb.: 2012_250_PE, *D.F. Morales-Briones & S. Uribe-Convers 219* (ID); 2015_171_MX, *D.F. Morales-Briones & P. Tenorio-Lezama 617* (ID). ***Lachemilla williamsii*** (L.M. Perry) Rothm.: 2013_402_BO, *D.F. Morales-Briones et al. 298* (ID).